

## Waving Display and Sound Production in the Courtship Behavior of *Uca pugilator*, with Comparisons to *U. minax* and *U. pugnax*<sup>1,2</sup>

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(Plates I-V; Text-figures 1-7)

### I. INTRODUCTION

**M**ALE fiddler crabs (Genus *Uca*) often exhibit movements of the enlarged major cheliped called "waving" or "beckoning" (Crane, 1957). In some species, the cheliped is also vibrated against the substrate to produce a series of sounds. The purpose of this study was to determine the role of waving display and sound production in the behavior of *Uca pugilator*. The behavior of this sound-producing species was compared with that of two other local species, *U. minax* and *U. pugnax*, from which sound production had not been reported. The influence of temperature, tide, light, darkness, sound playbacks, tactile stimuli and other crabs on waving display and sound production by test crabs was determined.

Comparative studies of waving in fiddler crabs have been published by Crane (1941.1, 1943.1, 1943.2), Peters (1955) and Altevogt (1955.1). Crane (1943.1) reported that each species had a waving display so characteristic that it could be used to distinguish between closely related forms. Similarity in waving display and in certain morphological features enabled her to formulate a tentative phylogeny of over thirty Pacific American species. She proposed that evolution within the genus involved movement from a stable, damp habitat only briefly exposed during low tide, to periodically dry habitats such as sloping mud or sand flats, beaches and banks of fresh water streams subject to seasonal drying.

The more specialized species showed the most complex waving displays. After completing a study of Indo-Pacific forms, Crane (1957) offered the following explanation to account for the evolution of waving display within the genus. In the "narrow front" species, the males exhibited "vertical waves" in which the major cheliped was raised and lowered without being flexed away from the body. In the "broad front" species, the cheliped was flexed laterally, away from the body, during the wave. The primitive narrow fronts that radiated from their center of distribution in the Indo-Malay region gave rise to the advanced broad front forms typical of Central and South America. Species of both groups reached their greatest complexity in waving display in relatively exposed habitats. The evolutionary trend to increase the conspicuousness of the wave of the male was expressed as follows. The size of the male, the amount of time devoted to waving and the tempo of the waving movement, particularly when a female approached, were increased. Special movements of the body and ambulatory legs, as well as the evolution of sound production associated with the wave, were developed. In addition, copulation, rather than taking place on the surface of the beach or in the female's burrow as in the narrow fronts, took place in the male's burrow where the female was enticed to follow the male by his initial waving overtures.

There has been disagreement in the literature concerning the function of waving display. Some authors (Muller, 1869; Darwin, 1871; Alcock, 1892, 1902; Pearse, 1914.1, 1914.2) believed that waving was utilized by the male to attract the female. Verway (1930), Hediger (1933, 1934) and Gray (1942) stated that waving had no courtship function but served to

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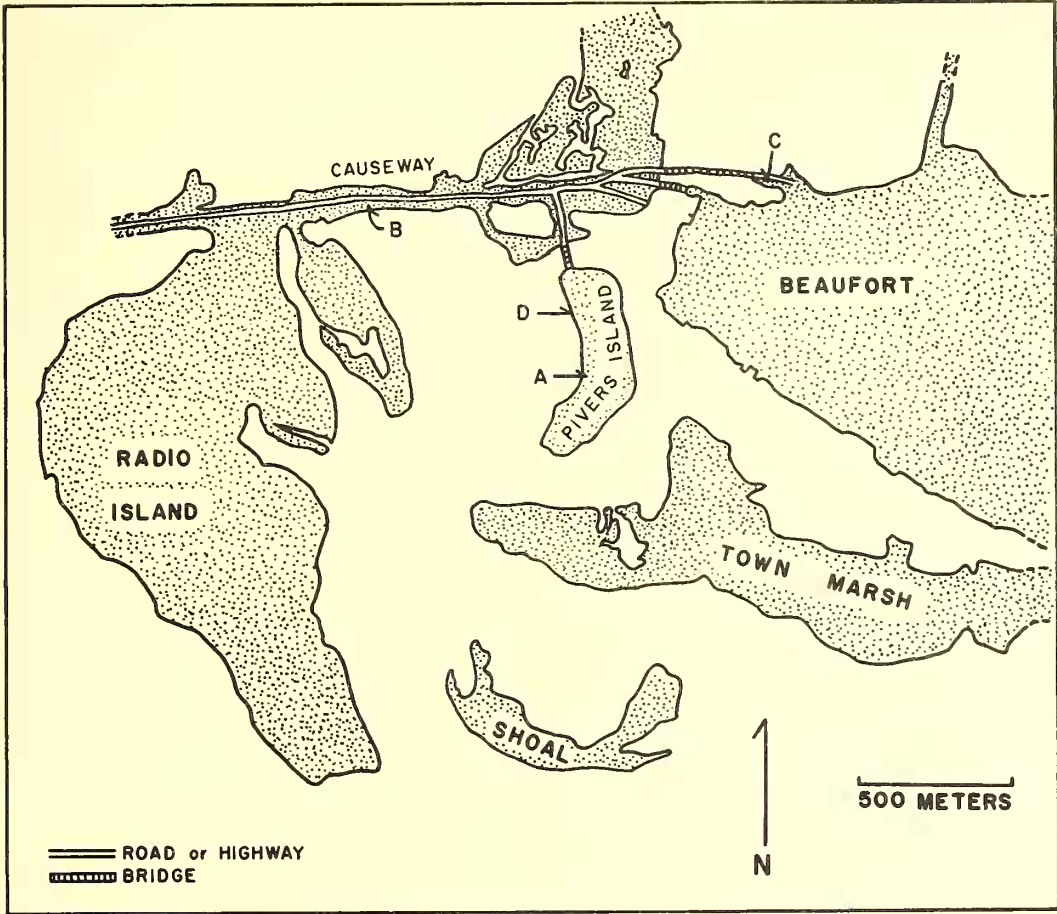
demarcate the burrow and surrounding area as the territory of the male. Altevogt (1955.1), studying *U. marionis* and *U. annulipes*, assumed that if waving demarcated a territory, the male should stay with his burrow "... for longer than just for an occasional visit or for one high tide." He marked males and found that between consecutive high tides they wandered many meters from one burrow to another. Some of the wandering males were observed to wave as they travelled. He concluded that waving probably was involved with courtship display and had no territorial function. He reaffirmed this view in other studies on the same two species and on *U. triangularis* (1955.2, 1957), as well as *U. tangeri* (1959). Crane (1958) also observed waving in *U. marionis* even when the male possessed no burrow and remarked that waving by non-territorial males was typical of primitive and semi-primitive species. Pearse (1912), studying several species at Manila, reported that males waved their claws frantically "... but they apparently do this to an equal extent whether females are present or absent and without any apparent reference to mating ..." However, he pointed out that his observations were not made during the breeding season. Several authors (Alcock, 1892; Symons, 1920; Johnson & Snook, 1927; Beebe, 1928; Matthews, 1930; Burkenroad, 1947; Salmon & Stout, 1962; Von Hagen, 1961, 1962) reported that the appearance of a female caused males to wave more rapidly, implying that waving was involved in courtship activity. Crane (1941.1) felt that "... waving is certainly carried on some of the time as a warning to other males and to delimit territory in some (but not all) species of *Uca*. On the other hand, in many, if not all species, waving definitely plays a large part in courtship ..." Schöne & Schöne (1963) also stated that waving was used in courtship and in aggressive interactions between males and based their views on studies of *U. pugilator* and *Goniopsis cruentata* in which waving also occurs.

The earliest observations on the waving display of North American forms were made by Pearse (1914.1), Swartz & Safir (1915) and Gray (1942), but species-specific differences in the displays were not reported until the publication of Crane's (1943.2) study of *U. pugilator*, *U. pugnax* and *U. minax*. Some of her observations on the waving display of *U. pugilator* were confirmed by Salmon & Stout (1962). Schöne & Schöne (1963) briefly compared the waving displays of *U. pugilator*, *U. rizophorae* and *U. annulipes*. Tashian & Vernberg (1958) utilized differences in waving movements, in addition to ecological and morphological cri-

teria, to indicate the species-specificity of *U. pugnax* and *U. rapax* (then considered subspecies) where their ranges overlapped in north-eastern Florida.

Aurivillius (1893) and Rathbun (1914) predicted on morphological grounds that stridulatory sounds could be produced by some species of *Uca*, but none have been reported. Dembowski (1925) saw male *U. pugilator* making a peculiar shivering movement with the major cheliped which resulted in sounds lasting from 1-3 seconds. The sounds produced by a crab near the burrow entrance resulted in the appearance of another crab on the surface, which defended its burrow. Crane (1941, 1943.1) described sound production by rapping of the pollex of the major cheliped against the substrate during the waving displays of six tropical American species of *Uca*. In most cases, the sounds were produced by excited males just before rushing into their burrows in response to the approach of a near-by female. A drum whirl ("Trommelwirbel") sound was reported in *U. tangeri* by Altevogt (1959, 1962) which was also produced by excited males, and studies by Von Hagen (1961, 1962) revealed that the sounds could be used in fights for possession of a burrow, as reported by Dembowski (1925) for *U. pugilator*. Two distinct types of sounds were produced by *U. tangeri*, the short whirl of 1-3 beats and the long whirl of 7-12 beats. The short whirl occurred when the male was temporarily obscured from the female by an obstruction in the field or mechanically prevented from waving by dense plant growth. The time between two short whirls was found to equal the time between two consecutive waves at the same temperature. The long whirl was produced by excited males just before entering their burrows, in response to the approach of a female, and by males at night in front of the burrow entrance of conspecifics. The long whirl caused the resident in the burrow to come out. If the resident was a female, copulation might follow. If it was a male, aggressive encounters ensued. Females were also able to produce the long whirl sound and did so in aggressive encounters involving defense of the burrow. The sounds could be produced in at least two ways. Males with intact major chelae produced sounds by rapping the substrate as described for other species of *Uca*. Males with small regenerating major chelae and females produced sounds by striking the substrate with alternate movements of each cheliped.

Sound production by rapidly waving males of *U. pugilator* was observed by Crane (1943.2) and described as a rapping movement similar to those she observed in tropical species. Burken-



TEXT-FIG. 1. Map of the area where studies were carried out. Populations of *Uca pugilator* were observed on the western beach of Pivers Island (A), on the South side of the Causeway (B) and Beaufort Basin (C). Populations of *U. pugnax* were studied at more muddy areas on Pivers Island (D) and near the North River (not shown on map) where colonies of *U. minax* were also observed, about seven kilometers from Beaufort. The Duke Marine Laboratory occupies the southern half of Pivers Island.

road (1947) did not believe rapping was utilized in sound production as he could detect no disturbance of the sand grains below the cheliped of a male *U. pugilator* that had just produced sounds. He reported that waving occurred during the day and sounds were produced at night and only during the day when excited males, inside their burrows, had been approached by a female. Burkenroad, and later Salmon & Stout (1962), hypothesized that the sounds substituted for waving when visual cues could no longer be utilized, i.e., at night and within the confines of the burrow.

## II. MATERIALS AND METHODS

All field observations and experiments were carried out from June 15 to July 28, 1962, and from March 21 to September 10, 1963, while

the author was at the Duke University Marine Laboratory, Beaufort, North Carolina. In 1962, several large colonies of *U. pugilator* were used for study on the western beach of Pivers Island (Text-fig. 1-A). These colonies were considerably reduced by March, 1963. Large numbers of *U. pugilator* were transferred from the southern beaches of the Causeway and from the North beach of Beaufort Basin (Text-fig. 1-B and C) to the western beach. By mid-May a colony of several thousand crabs had been reestablished on Pivers Island and the behavior of the transferred crabs did not appear to deviate from resident individuals in other locations. A small colony of *U. pugnax* was studied in the more muddy northwestern beaches of Pivers Island (Text-fig. 1-D). Additional observations were made on small and widely scattered colonies of

*U. pugnax* and *U. minax* located on the western side of the North River, seven kilometers from Beaufort.

All three species responded to the initial presence of an observer by rushing into their burrows. They usually reappeared on the surface within a few minutes and would exhibit apparently normal behavior as long as no sudden movement was made. By remaining motionless, it was possible to watch the crabs from distances of less than two meters. Movies of waving behavior were made with a Paillard-Bolex 16 mm. camera with 135 mm. telephoto lens to supplement drawings and to obtain more accurate temporal data. In some cases observations were made of male *U. pugilator* enclosed in 1.6 × 1.6 meter square house window screen pens, 20 cm. high. These crabs were observed for five minutes at 15-30 minute intervals throughout the day. Some observations, such as the rate of sound production or waving by individual males, were quantified in the field with the aid of stop-watch and counter. Temperature, tidal conditions and time of day were also noted.

Observations at night were made with the aid of a weak flashlight. During the breeding season, male crabs did not react to a weak light source for at least thirty seconds, but, as previously reported by Burkenroad (1947), bright light from strong flashlights induced some males of *U. pugilator* to wave at night. Female crabs of all three species appeared much more sensitive to light and immediately went into their burrows or moved away from the light source.

The colonies of *U. pugnax* and *U. minax* were not located near electrical outlets, therefore an Aiwa transistor tape recorder (Model TP-30) and microphone were used to record sounds of these species. The microphone was placed directly over the burrow containing the experimental crab. An Ampex tape recorder (Model 301, single tract), or a Magne recorder tape recorder mechanism (Model PT630-A) and recording and playback amplifier (Model PT63-J) were used to record sounds of *U. pugilator* on the western beach of Pivers Island. All recordings were made at tape speeds of 18.75 cm. per second (7.5 i.p.s.), and with the record level adjusted so that sounds peaked at no more than minus one on the VU meter of the tape recorder. When the tide was below the colony, an Argonne contact microphone (Model AR-17), enclosed in a Saran wrap covering to prevent damage from moisture and sand, was used to make recordings. The microphone was sensitive to substrate vibrations and relatively insensitive to air-borne sounds which made possible recordings virtually free of background noise. A

Chesapeake Instrument Corporation hydrophone (Model LF-310 with N-140 internal pre-amplifier) was used to make recordings when the crabs were submerged at high tide. Recordings were made by placing the contact microphone or hydrophone 2.5 cm. from the male's burrow entrance. A weight, usually a small shell from the beach, was placed on top of the contact microphone to ensure firm contact between the microphone and the substrate. The acoustical response of individual males was recorded in all experiments, but in order to obtain more data during the diel recordings, the sounds of two males located at least two meters apart, were recorded simultaneously. Differences in the pitch of their rapping sounds, probably due in part to local dissimilarities in the substrate, made it possible to distinguish between their sounds.

Sound playbacks were made by recording selected portions of sounds from tapes made in the field on a 15-second cartridge of a Mohawk Business Machine message repeater. The portion of the cartridge tape that stopped the playback every 15 seconds was removed so that playbacks were continuous. All playbacks were made through a University submergence-proof speaker (Model MM-2). The speaker was placed face down about 2.5 cm. from the crab and equidistant between the crab and the microphone. By adjusting the volume of the playback and monitoring with a tape recorder the sound intensity of the playback relative to the intensity of sounds produced by the test crab could be controlled. This procedure also enabled simultaneous recording of both sound playback and acoustical response of the crab. In control tests the speaker was placed by the crab's burrow but no sound was played back.

Experiments to determine if female *U. pugilator* would orient to sounds of conspecific males were carried out. A box 60 × 25 × 16 cm. high was constructed of 0.6 cm.-thick plywood and filled 7.5 cm. deep with sand. A speaker was placed faced down at each end of the box. The females were placed under a small cardboard box between the two speakers. After one minute of playback the cardboard box was lifted to release the female. One of the two speakers was chosen at random for the playback and each female was used only once. One minute after the female was released her position in the box was noted. Tests were carried out in darkness to eliminate possible visual cues, and at various times of the day. The intensity of the playback was comparable to that of males in the field.

Introduction experiments to male crabs on the surface of the beach during the day were made with the use of threads and probes as de-

scribed previously (Salmon & Stout, 1962). The procedure was slightly modified as follows. The thread was marked at 2.5 cm. intervals so that the introduced crab could be moved 15 cm. to either side of the male's burrow and at a speed of about 10 cm. per second. The probes were placed so that the introduced crab passed the test crab at known distances from its burrow. The test male was frightened into his burrow when the probes and introduced crab were placed. The experiment began one minute after he reappeared from the burrow. The effect of movement of a female on the behavior of a test male was determined by forcing the female to stand without lateral movement near the male for one minute. She was then pulled laterally back and forth before the male for a second minute and finally forced to remain without lateral movement for a third minute. The number of waves produced by the test male during each one minute period was quantified. In another series of tests the effect of non-moving females on male behavior was tested. The introduced female was kept hidden from the male behind a small sand barricade and then presented, but allowed no other movement. In a third series of tests the female was introduced at different distances from the male's burrow. In these tests a microphone was placed near the burrow so that tape recordings could be made during the introduction. This procedure enabled quantification of both the number of sounds and waves made by the male during the test.

Some experiments involved the effect of changes in light and darkness. A small desk lamp with a 100 watt incandescent bulb was used to test the effect of light on sound production by male *U. pugilator* at night. After a contact microphone was positioned the lamp was placed about one meter from the crab so that the light would shine directly into the burrow. The sounds produced by the crab were recorded for two minutes before and for two minutes during the time when the light was turned on. Two wooden boxes, 20 × 15 × 14 cm. high, were constructed of 0.6 cm.-thick plywood without top or bottom. The open top of one box was covered with black plastic sheeting which made it lightproof from below. The other box was covered with Saran wrap. After microphones were placed near the burrows of two males, the boxes were placed over both the burrows and the microphones. These boxes were used in simultaneous recordings of pairs of male *U. pugilator* during diel experiments. Two larger boxes, 70 × 25 × 14 cm. high, covered either with black plastic or Saran wrap, were used in sound playback experiments during the day. A speaker

was placed face down, 2.5 cm. from the box, for these tests.

A single sound consisted of several (3-14) pulses, each one of which was produced as the cheliped of the crab was rapped against the substrate. The sounds were usually produced in a series with the intersound intervals much greater than the interpulse intervals. A Kay Electric Company Sonograph Model Recorder (B) was used to measure the sound duration in milliseconds, the number of pulses per sound and the frequency spectra of the sounds. A Brüel and Kjaer Level Recorder (Type 2305) was used to measure intersound intervals and in some cases the number of pulses per sound.

In order to compare the interpulse intervals of different sounds, the following procedure was utilized. For each sound analyzed, the sound duration in milliseconds was divided by the number of pulses in the sound. The resulting value, referred to as the sound duration to pulse ratio, gave a relative measure of the interpulse interval of each sound in samples produced under different experimental conditions or at different temperatures. Means of the sound duration to pulse ratio, number of waves, number of sounds, or number of pulses per sound were compared statistically with t-tests. Deviations from the mean under different experimental conditions were analyzed with F-tests. The .05 significance level was chosen. The sign test was used to analyze some of the data when parametric statistics were not applicable.

Changes in the acoustical behavior of male crabs during introduction experiments were brief in duration (10-20 seconds), probably because the female crabs used in the test were not sexually receptive to the males. Therefore, the acoustical behavior of males 15 seconds immediately before and during the introduction tests were compared. In some cases the last 5 sounds before and the first 5 sounds during a test were compared. These sounds were usually produced within 15 seconds before and during the test.

### III. RESULTS

#### A. SEASONAL CHANGES IN COURTSHIP ACTIVITY

During the winter, temperate zone fiddler crabs hibernate beneath the surface (Crane, 1943.2), presumably in their burrows. In 1963, male and female *U. pugilator* were first observed on the beach at Pivers Island in early March (Mr. Clel Bartell, personal communication). Field observations by Mr. Bartell in early March and by me later in the month indicated that almost no courtship was exhibited although many crabs emerged from their burrows during the day when the tide was low. Feeding, burrow

repair and occasional aggressive encounters characterized their behavior at this time. Aggressive interactions frequently took place between neighboring resident males or between residents and intruders and consisted of shoving and pushing movements with the chelae and body. Interlocking of the major chelae in bouts between males, followed by twisting and pulling movements, occasionally took place. One or two males each day were observed to wave three or four times at a near-by female but the movement was slow and the large chela was barely elevated. Air temperatures during many March afternoons rose to 25°C. and crabs often exhibited active courtship at colder temperatures later in the season. By early April, waving activity was prevalent in the colonies located at Beaufort Basin, the Causeway and Pivers Island.

During March and part of April, no nocturnal sound production by *U. pugilator* was heard in the field. When low tide occurred at night only a few crabs opened up their burrows to the surface. Air temperatures at night ranged from 10° to 15°C. during this time. Sound production by males was first heard the night of April 17 at Beaufort Basin and was prevalent in all local colonies during low tides at night by the end of that month. Waving during the day and sound production at night continued until late August. By September 10, when observations ended, sound production at night had stopped and waving was observed only on rare occasions. Temperatures were still comparable to those earlier in the season. The reduction in waving and sound production appeared to take place within a one-week period.

## B. RESULTS OF STUDIES ON WAVING BEHAVIOR

1. *Differences in waving display between the three species.* The topography of a single wave in *U. minax*, *U. pugnax*, and *U. pugilator*, all drawn from individual frames of 16 mm. film at various times after the wave began (indicated below each drawing), is shown in Text-fig. 2. The waves of *U. pugnax* and *U. pugilator* were made by males when no female was present. Only one male *U. minax* could be filmed as he was courting a near-by female. Under these conditions the duration of his wave, indicated at 2.5 seconds in Text-fig. 2, was about two to three times as fast as those exhibited by four other males when no female was present. The duration of waves shown by 15 male *U. pugnax* ranged from 2.5 to 5.0 seconds and by 20 male *U. pugilator* from 1.0 to 2.0 seconds.

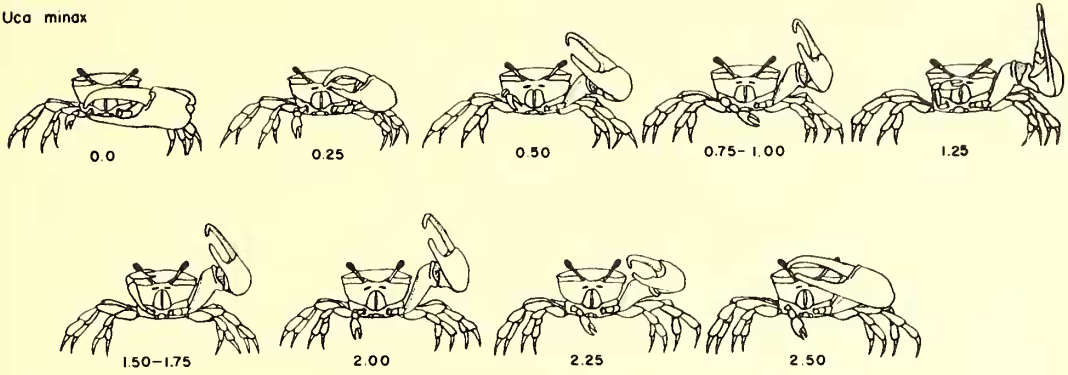
Other differences between the waving displays of the three species were observed in the field. The minor chela moved asynchronously with re-

spect to the major during waves by five male *U. minax*. In three male *U. pugnax* the minor chela waved twice to a single wave of the major; it might move synchronously with the major as shown in Text-fig. 2, or rarely it was not moved at all. In 20 male *U. pugilator* the minor chela moved synchronously with the major, or rarely was not moved at all. The major chela was raised and lowered once in a series of four to seven jerks in *U. minax* and without any associated lifting movements of the ambulatories. In *U. pugnax* the major chela was raised, extended laterally and returned immediately to the front of the body in a smooth continuous movement. The second, third, or both pairs of ambulatories on both sides of the body were raised and lowered just before and after the major chela reached its maximum lateral extension. In *U. pugilator* the major chela was raised vertically, held at a maximum elevation for a fraction of a second, then extended laterally and returned to the front of the body. The ambulatories on the side opposite the major chela were raised once as the chela was extended laterally from its maximum elevation.

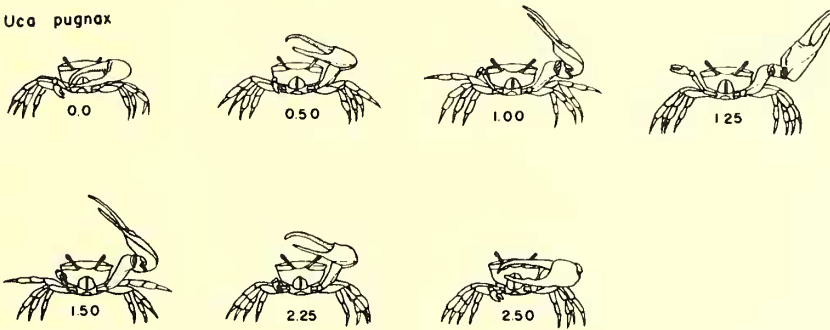
In all three species the approach of a female caused an increase in the rate of waving by male crabs. When the female approached to within 4-6 cm. of the male's burrow the form of the wave changed as follows. The lateral extension of the male's claw during each wave no longer occurred. Rather, the claw was vertically lifted, and then lowered before the body as in the narrow front species. During this stage of courtship male *U. pugilator* usually vibrated the claw against the substrate to produce a series of sounds. The vibration movements occurred between two consecutive waves, when the claw was lowered from its maximum vertical elevation, and just before it was raised again. No sound production was observed in *U. minax* or *U. pugnax* during this stage of courtship.

The three species showed differences in male group display behavior. Waving by *U. pugnax* and *U. minax* was infrequent and of short duration when no female was present. In contrast, groups of male *U. pugilator* waved almost continuously in the absence of females except for brief periods of feeding, fighting and burrow repair. Further, males in any one area of the colony often began to wave rapidly in groups, when no female was present. On other occasions similar group waving by males started when one male, in response to an approaching female, began to produce sounds. Other males within a one meter distance would then increase their rate of waving even after the female had moved away or had entered the sound-producing male's burrow. The sounds were also cor-

*Uca minax*



*Uca pugnax*



*Uca pugilator*



TEXT-FIG. 2. Single waves of *Uca minax* (top two lines), *U. pugnax* (middle two lines) and *U. pugilator* (bottom line). Sequences start at left and continue to the right through consecutive movements. The time (in seconds) below each sequence is the time from the beginning of the wave. For further explanation, see text.

related with the sudden appearance of nearby males, previously in their burrows, on the surface of the beach. These newly emerged males immediately joined other males in group waving activity.

2. *Results of introduction experiments.* The average number of waves by 30 male *U. pugilator* 5 seconds before and 5 seconds during introduction of conspecific females from behind sand barricades is shown in Table 1. The average rate of waving nearly doubled during the 5-second period of the introduction. The increase was statistically significant at the .01 level. The effect of movement by females on the waving by males is shown in Table 2. The mean rate of waving more than doubled when the female was moved after she had previously been held without lateral movement before the male. The rate was greatly reduced after lateral movement. When com-

pared with t-tests, the mean number of waves during all three periods was found to differ significantly from one another. During periods when the females were held motionless they were attacked by 13 of the 30 test males. As soon as the female was moved the attacking males immediately began to wave at a high rate.

TABLE 1. THE MEAN NUMBER AND STANDARD DEVIATION OF WAVES BY 30 MALE *Uca pugilator* 5 SECONDS BEFORE AND DURING INTRODUCTIONS IN FRONT OF THEIR BURROWS OF CONSPECIFIC FEMALES FROM BEHIND SAND BARRICADES

	Before Introduction	During Introduction	t-Value
Mean	2.7	5.9	45.07*
S D	0.8	1.0	

\*Means differ significantly at the .01 level.

TABLE 2. THE MEAN NUMBER AND STANDARD DEVIATION OF WAVES BY 30 MALE *Uca pugilator* ONE MINUTE BEFORE, DURING AND AFTER CONTINUOUS MOVEMENT OF A CONSPECIFIC FEMALE BEFORE THEIR BURROWS

	Before Movement (A)	During Movement (B)	After Movement (C)	t-Value
Mean	12.8	28.2	3.9	t(AxB) = 5.19* t(AxC) = 3.72*
S D	11.2	11.8	7.0	t(BxC) = 10.13*

\*Means differ significantly at the .01 level.

The effect of movement of other female *Uca* was also determined and the results are shown in Table 3. In all cases, there was a significant increase in the mean rate of waving during the period when the female was moved. The two female *U. rapax* used in these tests (obtained from Florida), elicited more waves from males than did females of local species.

More than twenty male *U. pugilator* were released singly into areas of the colony containing conspecific resident males. The released males wandered through the colony, approached resident males and females, and tried to enter their burrows. In all approaches by released intruding males, resident males stopped waving and assumed typical aggressive postures with the major chela oriented toward the intruding males. When the intruders moved away the residents started waving again. In other cases ritualized fighting, consisting of pushing and twisting movements of the interlocked major chelae, would take place. In over 80 per cent of these aggressive

encounters the resident males retained their burrows. Resident males were never observed to increase their waving rates when approached by other males unless the intruding males were very small, possessed a small major chela (typical of males regenerating a new claw) or approached with their bodies between their major chela and the residents.

3. Results of sound playback experiments. The results of sound playback of 56 sounds per minute to 30 male *U. pugilator* are shown in Table 4. The mean rate of waving by males before the playback was low, probably because of the presence of the speaker near their burrows. During the one minute playback the mean rate of waving increased almost four times. The mean rate after the playback was reduced but still significantly greater than the rate before the playback. The sound playback of 56 sounds per minute contained the greatest number of sounds ever recorded from a male during a 15-second period (14 sounds per 15 seconds) and probably was

TABLE 3. THE MEAN NUMBER AND STANDARD DEVIATION OF WAVES BY 10 DIFFERENT MALE *Uca pugilator* DURING ONE MINUTE PERIODS BEFORE, DURING AND AFTER CONTINUOUS MOVEMENT OF SINGLE FEMALE *Uca* spp. BEFORE THEIR BURROWS

Species of Female	Female Carapace Width (cm.)		Before Movement (A)	During Movement (B)	After Movement (C)	t-Value
<i>U. minax</i>	1.7	Mean:	6.5	20.5	5.2	t(AxB) = 2.64*
		S D:	5.9	15.7	16.5	t(AxC) = 0.26 t(BxC) = 2.70*
<i>U. minax</i>	1.8	Mean:	9.5	19.6	6.9	t(AxB) = 2.30*
		S D:	12.9	8.6	7.5	t(AxC) = 0.62 t(BxC) = 3.53†
<i>U. rapax</i>	2.0	Mean:	11.8	30.5	10.6	t(AxB) = 3.56†
		S D:	9.2	13.9	12.9	t(AxC) = 0.00 t(BxC) = 3.32†
<i>U. rapax</i>	1.7	Mean:	10.4	40.7	10.6	t(AxB) = 5.88†
		S D:	9.0	13.9	9.6	t(AxC) = 0.02 t(BxC) = 5.84†
<i>U. pugnax</i>	1.3	Mean:	8.2	22.4	11.0	t(AxB) = 2.69†
		S D:	12.2	11.4	7.8	t(AxC) = 0.63 t(BxC) = 2.61*

\*Mean during movement of female (B) differs significantly from other means (A or C) at the .05 level.

†Mean during movement of female (B) differs significantly from other means (A or C) at the .01 level.



TABLE 4. THE MEAN NUMBER AND STANDARD DEVIATION OF WAVES BY 30 MALE *Uca pugilator* BEFORE, DURING AND AFTER SOUND PLAYBACK OF 56 SOUNDS PER MINUTE

	Before Playback (A)	During Playback (B)	After Playback (C)	t-Value
Mean	4.4	17.2	8.0	$t(AxB) = 8.76^*$ $t(AxC) = 2.58^*$
S D	4.1	6.8	6.6	$t(BxC) = 5.29^*$

\*Means differ significantly at the .01 level.

near to the maximum rate of sound production for the species.

Males frightened into their burrows were tested for emergence time with and without sound playback and the results are shown in Table 5. With no sound playback, six males took a minute or more to emerge and seven did not emerge within the two-minute test period. When sounds were played back to another 20 males, 16 emerged within one minute after the playbacks began and only one male remained in his burrow during the entire test period.

### C. RESULTS OF STUDIES ON SOUND PRODUCTION

1. *Results of field observations.* The behavior of 25 male *U. pugilator* as they were approached by females is shown in Table 6-A. In all observations, approach by the female resulted in sound production by the male. If the female approached slowly, sound production by males was preceded by many (15-25) waves delivered at a high rate. This type of approach by females was most often observed. When females approached quickly or in several short spurts, very few waves were exhibited by the males. The behavior of females once at the male's burrow is shown in Table 6-B. In most cases the females entered the burrow but left immediately. In a few observations they completely by-passed the burrow or entered and remained with the male for over two minutes.

At night, males in the upper third of the beach at Pivers Island produced sounds almost continuously when the tide was low. There appeared to be no monthly changes in this behavior, as recordings of many males in the same areas of the beach were obtained on consecutive nights when the tide was low. However, no observations on the acoustical behavior of individual males throughout the summer were made. Sound production at night was inhibited when there were strong winds and rain. The number of sound-producing crabs increased while the tide was receding and reached a maximum on the incoming tide. The transition from waving to sound production was observed when low tides coincided with sunset. Within 30 minutes after sunset, waving stopped. Almost all male crabs

would enter their burrows and remain there for about one hour. At first, only a few males would produce a brief series of sounds. But within one hour after sunset most of the males were producing sounds from inside their burrows. During the second hour after sunset the males would move up to the entrances of their burrows where they continued to produce sounds until the incoming tide and/or sunrise resulted in cessation of this behavior. One sound-producing male in position and the impression made by the rapping major chela in the sand is shown Plate I. The

TABLE 5. THE TIME OF EMERGENCE IN SECONDS FROM THEIR BURROWS OF 20 MALE *Uca pugilator* WITH AND WITHOUT SOUND PLAYBACK OF 56 SOUNDS PER MINUTE FOR TWO MINUTES<sup>1, 2</sup>

Male Number	Without Sound Playback (Controls)	With Sound Playback (Experimentals)
1	DNE*	50
2	15	65
3	35	20
4	70	35
5	105	90
6	DNE	15
7	100	21
8	120	35
9	35	30
10	DNE	45
11	15	45
12	20	DNE*
13	50	14
14	60	25
15	118	90
16	50	20
17	DNE	25
18	DNE	30
19	DNE	7
20	DNE	15

\*DNE: Did not emerge from their burrows within the two-minute test period.

<sup>1</sup>Twenty different males, tested alternately, were used for each series.

<sup>2</sup>The number of control crabs that DNE is significantly greater than the number of experimentals at the .01 level (Chi-square = 5.62). The number of experimental crabs emerging sooner than control crabs is significantly greater at the .01 level (Sign test value = 3).

TABLE 6. A SUMMARY OF THE COURTSHIP BEHAVIOR OF MALE AND FEMALE *Uca pugilator* DURING THE DAY

A. The Approach of the Female to the Male			
Behavior of Female	Response of Male	Number of Observations	
Slowly approaches the male	Many waves, followed by sound production at the burrow entrance	18	
Approaches the male quickly	Few waves, followed by sound production inside the burrow	3	
Female approaches the male in 4-5 short spurts	Few waves, followed by sound production outside or inside the burrow	4	
B. The Behavior of Females at the Male's Burrow			
	By-Passes Burrow	Enters Burrow, Then Leaves Immediately	Remains in Burrow Over 2 Minutes
Number of Observations	9	21	4

male's body was either slightly elevated or the ventral surface sometimes touched the ground. The ambulatories on the major side were extended and spread. The movement of the chela before, during and after one rap against the substrate is shown in Text-fig. 3 A-C. A single sound as defined here was composed of several (3-14) pulses, each one of which was produced as the chela struck the substrate.

The results of per minute tallies of sounds for 15 minutes by eight males at night are shown in Table 7. All but two males produced sounds within each minute during the entire 15-minute period. The range in per minute production by each crab varied from 6 to 22 sounds during these observations.

The mean, first standard deviation, and range of per minute sound production by samples of males at different air temperatures is shown in

Text-fig. 4. The mean number of sounds produced per minute increased with higher temperatures although there was considerable variation in the number of sounds produced by any one crab within each sample. Five sounds from recordings of ten different males at 14°, 18.5° and 24° C. were selected at random and analyzed sonographically. The sound duration, number of pulses per sound and sound duration to pulse ratio were calculated for each sound. The results are shown in Text-fig. 5 A-C. Sounds produced at higher temperatures were of shorter duration and had smaller sound duration to pulse ratios. There was no significant difference between the mean number of pulses per sound at the three temperatures. Sonograms of one sound produced at each temperature are shown in Plate II. The mean time interval between sounds of 20 male *U. pugilator* at 24° C. was found to be 2.9 sec-

TABLE 7. THE NUMBER OF SOUNDS PER MINUTE PRODUCED BY EACH OF 8 MALE *Uca pugilator* AT NIGHT DURING A 15-MINUTE PERIOD

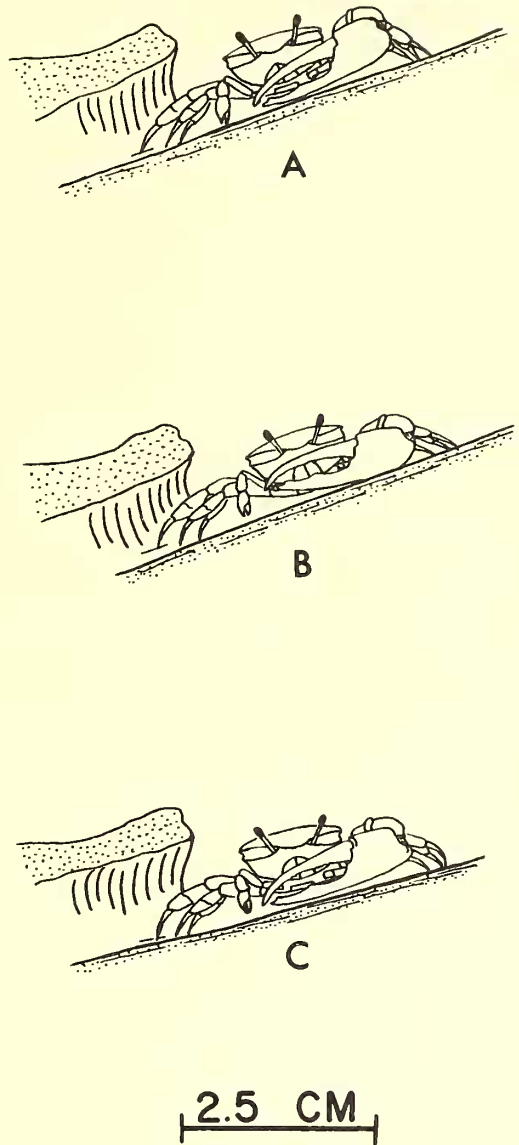
Time (in Minutes)	Male Number							
	1	2	3	4	5	6	7	8
1	26	13	18	19	32	26	24	25
2	25	21	21	22	35	22	20	22
3	25	18	22	20	31	22	18	19
4	23	9	15	20	28	23	20	24
5	29	0	21	10	28	21	20	25
6	26	8	18	14	27	28	19	25
7	29	14	16	23	26	9	5	16
8	29	11	2	3	26	22	17	19
9	24	15	2	6	25	16	23	21
10	25	11	0	14	23	22	17	22
11	29	14	0	17	20	20	20	25
12	27	22	0	19	27	20	19	21
13	23	19	0	16	25	21	18	18
14	25	19	0	16	26	22	19	18
15	23	16	11	17	28	14	20	26
Range:	23-29	0-22	0-22	3-23	20-35	9-28	5-24	16-26

onds with a range of 1.8 to 5.2 seconds. The average standard deviation was 1.65 with a range from 0.5 to 4.1.

Resident male *U. pugilator* at night, when touched by another crab, increased their rate of sound production while simultaneously moving 6-20 mm. into their burrows. This behavior was accompanied by rapid and repeated extension and retraction movements of the ambulatories on the side of the crab toward the burrow entrance. If the intruding crab followed the resident into the burrow, the resident's ambulatories would touch him when they were extended. The resident responded to this contact by moving still farther into his burrow and producing a rapid series of five to ten sounds. If the ambulatories did not touch the intruding crab, the resident stopped producing sounds and moved toward the burrow entrance. Both males and females were observed to release this behavior in resident males but only females, four in total, were ever observed to move into the burrow of a sound-producing male. An intruding male either moved away from the resident's burrow or struck the resident sharply with the major chela, which caused the resident to stop sound production and adopt defensive postures. Aggressive behavior in resident males at night could be elicited in a few instances by striking the male sharply with the flat surface of an autotomized chela from another male. Sound production at a high rate and associated ambulatory movements could be elicited by gently touching the resident male with an autotomized leg of another crab, a pencil point, a blunt wooden stick or a leaf tip. The results of tactile stimulation of male *U. pugilator* with a leaf of *Spartina* are shown in Table 8. Contact between the leaf and the crab's leg, dorsal or posterior parts of the carapace, or major chela usually resulted in sound production at a high rate. There was a slight tendency for males to respond aggressively to gentle tactile stimulation of the major chela.

The rate of sound production by groups of males was also observed to increase when a nearby male, probably due to tactile stimulation by another crab, increased his rate of sound production. In addition, previously silent males in the vicinity would begin to produce sounds.

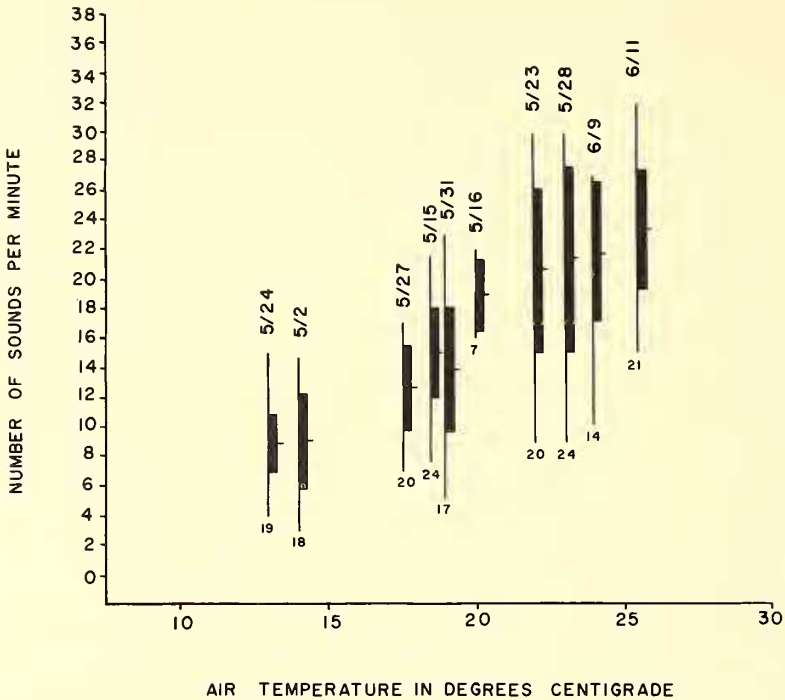
2. *Results of introduction experiments.* Female *U. pugilator* were introduced during the day at 2.5, 5.0, 7.5 and 10.0 cm. distances from the burrows of groups of ten conspecific males. The results are shown in Text-fig. 6. The males produced many sounds at the burrow entrance and few waves when the females were introduced at 2.5 cm. from the burrow. As the females were introduced farther from the burrow,



TEXT-FIG. 3. Drawings of a male *Uca pugilator* producing sounds just outside the entrance of his burrow. A-C: Movements of the major chela before (A), during (B) and after (C) one rapping movement of the chela against the sand.

the males produced many waves but progressively fewer sounds.

The number of sounds produced by 30 male *U. pugilator* 15 seconds before and during introduction of conspecific males and females into their burrows is shown in Table 9. During the day none of the males produced any sounds before the introduction but at night all males were rapping continuously before the test. The test males produced about the same number of sounds regardless of the sex of the introduced



TEXT-FIG. 4. The correlation between temperature and the rate of sound production by male *Uca pugilator* during 1963. In each sample, the vertical line indicates the sample range; the number below, the sample size in numbers of animals; the horizontal line, the mean; and the broad portion of the line, the first standard deviation on each side of the mean. The samples were obtained from one-minute tape recordings or direct observation in the field. The month/date when the data was recorded is shown above each sample.

crab. The average rate of sound production during nocturnal introductions was significantly greater than the average rate before introductions and was similar to the rate during day-time introductions. The last 5 sounds produced by 30 male *U. pugilator* before, and the first 5 sounds during, nocturnal introductions of conspecific females were chosen for analysis. The mean number of pulses and variance in pulse number before and during the introduction are shown in Table 10. There was no significant difference between the mean number of pulses but the variance in pulse number per sound was greater dur-

ing the introduction. One of the last 5 sounds before and one of the first 5 sounds during introductions of females to 15 male *U. pugilator* were selected at random and the sound duration to pulse number ratio was compared. The results are shown in Table 11. The mean ratio after the introduction was significantly less than the ratio before introduction, reflecting the decrease in interpulse intervals after the introduction. A sonogram of two sounds produced by the same male before and after the introduction of a female is shown in Plate III and illustrates the

TABLE 8. THE RESPONSE AT NIGHT BY MALE *Uca pugilator* TO TACTILE STIMULI WITH A LEAF OF *Spartina* ON VARIOUS PARTS OF THE BODY<sup>1</sup>

Place of Stimulation	Number of Responses Observed		
	High Rate Sound Production	Aggressive Response	Goes Into Burrow
Ambulatories	18	2	0
Face of Chela	14	5	1
Dorsal Carapace	17	0	3
Posterior Carapace	16	1	3

<sup>1</sup>Twenty different males were used in each test.

TABLE 9. THE MEAN NUMBER AND STANDARD DEVIATION OF SOUNDS PRODUCED BY 30 MALE *Uca pugilator* 15 SECONDS BEFORE AND DURING INTRODUCTION OF CONSPECIFIC MALES AND FEMALES INTO THEIR BURROWS

Sex of Introduced Crab	Time of Introduction	Before Introduction	After Introduction	t-Value
Female	Day	Mean:	0.0	10.7
		S D:		5.5
Male	Day	Mean:	0.0	10.6
		S D:		6.9
Female	Night	Mean:	5.9	10.2
		S D:	2.4	3.4
Male	Night	Mean:	5.0	8.8
		S D:	2.1	4.3

\*Mean number of sounds during introduction is significantly greater than mean before introduction at the .01 level.

reduction in interpulse intervals of sounds produced during the introduction.

Male *U. pugnax* produced sounds when a total of 18 females (14 *U. pugnax* and 4 *U. pugilator*) and 7 conspecific males were introduced into their burrows during the day. From 3 to 16 sounds were produced one minute after the introduction. The sound duration, pulse number per sound and interpulse intervals of the sounds were highly variable. Some sounds consisted of only one or two pulses and lasted less than a second while others consisted of up to 30 pulses and lasted over 5 seconds. The same crab produced sounds of long and short duration during a single recording. The movements involved in sound production were never observed, as the test male was always deep in his burrow and hidden by the introduced crab. No sounds were made by the test males until the introduction of another crab. A sonogram of these sounds, which seemed similar to stridulation sounds, is shown in Plate IV.

TABLE 10. THE MEAN NUMBER AND VARIANCE OF PULSES PER SECOND PRODUCED BY 30 MALE *Uca pugilator* BEFORE AND DURING INTRODUCTION OF CONSPECIFIC FEMALES<sup>1</sup>

	Before Introduction	During Introduction
Mean	6.7	7.1*
Variance	9.37	24.63†

<sup>1</sup>The last five sounds before and the first five sounds during the introduction of the female were chosen for analysis.

\*No significant difference between means ( $t = 0.08$ ).

†Variances differ significantly at the 0.1 level ( $F = 2.63$ ).

On two occasions male *U. pugnax* produced rapping sounds much like those of *U. pugilator* but at a much slower rate (3-5 pulses per 5 seconds). Unfortunately no tape recordings of these sounds were obtained.

Introduction of female *U. pugilator* into the burrows of 30 conspecific females resulted in the production of two sounds by one female. One of the sounds consisted of 40 pulses and lasted 12 seconds; the other, of 73 pulses and lasted 29 seconds. A sonogram of a portion of one of the sounds is shown in Plate IV. Another female, nudged roughly with a stick at night, assumed a defensive posture and hit the substrate with alternate movements of her two minor chelae for a few seconds before rushing into her burrow. The sounds from this female were similar to those recorded during the day.

No sounds were produced by male *U. minax* in response to introductions of other crabs.

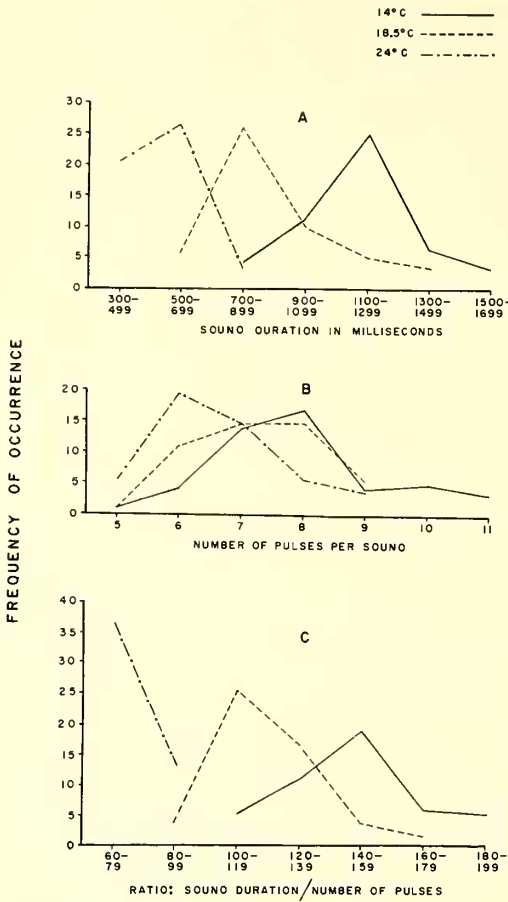
3. Results of sound playback experiments. The acoustical response of 20 male *U. pugilator* at

TABLE 11. THE MEAN AND STANDARD DEVIATION OF THE SOUND DURATION TO PULSE RATIO OF ONE SOUND PRODUCED BY 15 MALE *Uca pugilator* AT NIGHT BEFORE AND DURING INTRODUCTION INTO THEIR BURROWS OF A CONSPECIFIC FEMALE<sup>1</sup>

	Before Introduction	During Introduction	t-Value
Mean:	72.01	65.31	3.200*
S D:	7.6	9.8	

<sup>1</sup>One of the last five sounds before and one of the first five sounds during the introduction of a female to a male were selected at random for analysis.

\*Means differ significantly at the .01 level.



TEXT-FIG. 5. The sound duration in milliseconds (A), number of pulses per sound (B) and the ratio of the sound duration to the number of pulses (C) of five sounds selected at random from those produced by each of ten males at 14°, 18.5° and 24° C. All are plotted against frequency of occurrence. The procedures utilized to make this analysis are described under Materials and Methods.

night before, during and after one minute of sound playback at different rates is shown in Table 12. The average rate of sound production by males during the playback of 24 and 56 sounds per minute was significantly greater than the rate before and after the playback. With playbacks of 48 sounds per minute, the average rate after the playback differed significantly from the average rate before the playback. When the tape of 56 sounds per minute was reversed before playback, the males produced a significantly greater number of sounds during the playback than they did before the playback. The other mean rates of sound production during experiments did not differ significantly.

The effect of sound playback at night on silent males previously frightened into their burrows is

shown in Table 13. Nine of 15 males not receiving sound playbacks during the four-minute test period remained silent and all but two produced no sounds for one minute. One of 15 males receiving sound playbacks remained silent and all but two males produced sounds within one minute after the playback began. The increase in mean number of sounds produced by males receiving the playback was significant at the .01 level.

Playbacks of 16 and 24 sounds per minute were made at night to male *U. pugilator* for a three-minute period to determine if the males would synchronize their sounds with those of the playback. The results are shown in Table 14. There was no significant difference in the mean rate or between variances of the sounds produced during and after the playback.

The results of sound playbacks to single males under light-proof and clear-topped boxes during the day are shown in Table 15. No males produced sounds under either box one minute before the playback, probably because the experiment began within a few seconds after the box had been placed over the crabs' burrows. During the playback there was a significant increase in the mean number of sounds produced by males under the light-proof box. During the one minute period after the playback the males under the light-proof box continued to produce a greater number of sounds than those under the clear-topped box. When the light-proof box was placed over the burrows of 11 other males, but without sound playback, the males produced no sounds for at least three minutes.

A total of 54 female *U. pugilator* was tested in the laboratory with playbacks of sounds from conspecific males to determine if they would be attracted to the sound source (See MATERIALS AND METHODS for procedure). Of these, 15 did not move from the center of the box during the playback. All the other females moved to and remained against the right or left side of the box, behind one of the two speakers. A total of 25 females moved to the experimental speaker through which sounds were emitted while 14 moved to the silent control speaker. The preference for the experimental speaker was not significant at the 0.5 level ( $\text{Chi-square}=3.10$ ).

#### D. EFFECT OF LIGHT AND DARKNESS ON SOUND PRODUCTION AND WAVING BEHAVIOR

The results of three days of observations on the behavior of male *U. pugilator* surrounded by screen pens are shown in Table 16. Aggressive interactions between males, feeding behavior and burrow repair were consistent patterns of behavior occurring frequently during the day



TABLE 12. THE MEAN NUMBER AND STANDARD DEVIATION OF SOUNDS PRODUCED BY 20 MALE *Uca pugilator* AT NIGHT BEFORE, DURING AND AFTER ONE MINUTE OF SOUND PLAYBACK AT DIFFERENT RATES AND AT AN INTENSITY OF ONE-HALF THAT OF THE MALE'S SOUNDS

Number of Sounds Per Minute in Playback		Before Playback (A)	During Playback (B)	After Playback (C)	t-Value
Control (No Playback)	Mean:	21.0	17.9	18.9	t(AxB) = 1.24 t(AxC) = 0.71 t(BxC) = 0.33
	S D:	7.6	8.2	10.8	
16	Mean:	15.5	18.3	16.3	t(AxB) = 1.85 t(AxC) = 0.68 t(BxC) = 1.37
	S D:	3.9	5.5	3.6	
24	Mean:	20.8	25.5	21.6	t(AxB) = 2.83* t(AxC) = 0.34 t(BxC) = 2.12*
	S D:	6.9	8.4	7.8	
32	Mean:	20.7	20.6	19.4	t(AxB) = 0.02 t(AxC) = 0.52 t(BxC) = 0.47
	S D:	5.6	7.1	8.7	
40	Mean:	20.5	19.6	20.7	t(AxB) = 0.35 t(AxC) = 0.08 t(BxC) = 0.39
	S D:	6.3	9.5	8.5	
48	Mean:	24.4	25.2	28.9	t(AxB) = 1.35 t(AxC) = 3.42† t(BxC) = 1.78
	S D:	5.9	7.7	6.1	
56	Mean:	16.9	29.6	17.9	t(AxB) = 6.61† t(AxC) = 0.56 t(BxC) = 6.69†
	S D:	6.1	6.0	5.0	
56 (Reverse)	Mean:	18.6	25.3	21.5	t(AxB) = 3.14* t(AxC) = 1.12 t(BxC) = 1.11
	S D:	6.7	11.9	8.2	

\*Means differ significantly at the .05 level.

†Means differ significantly at the .01 level.

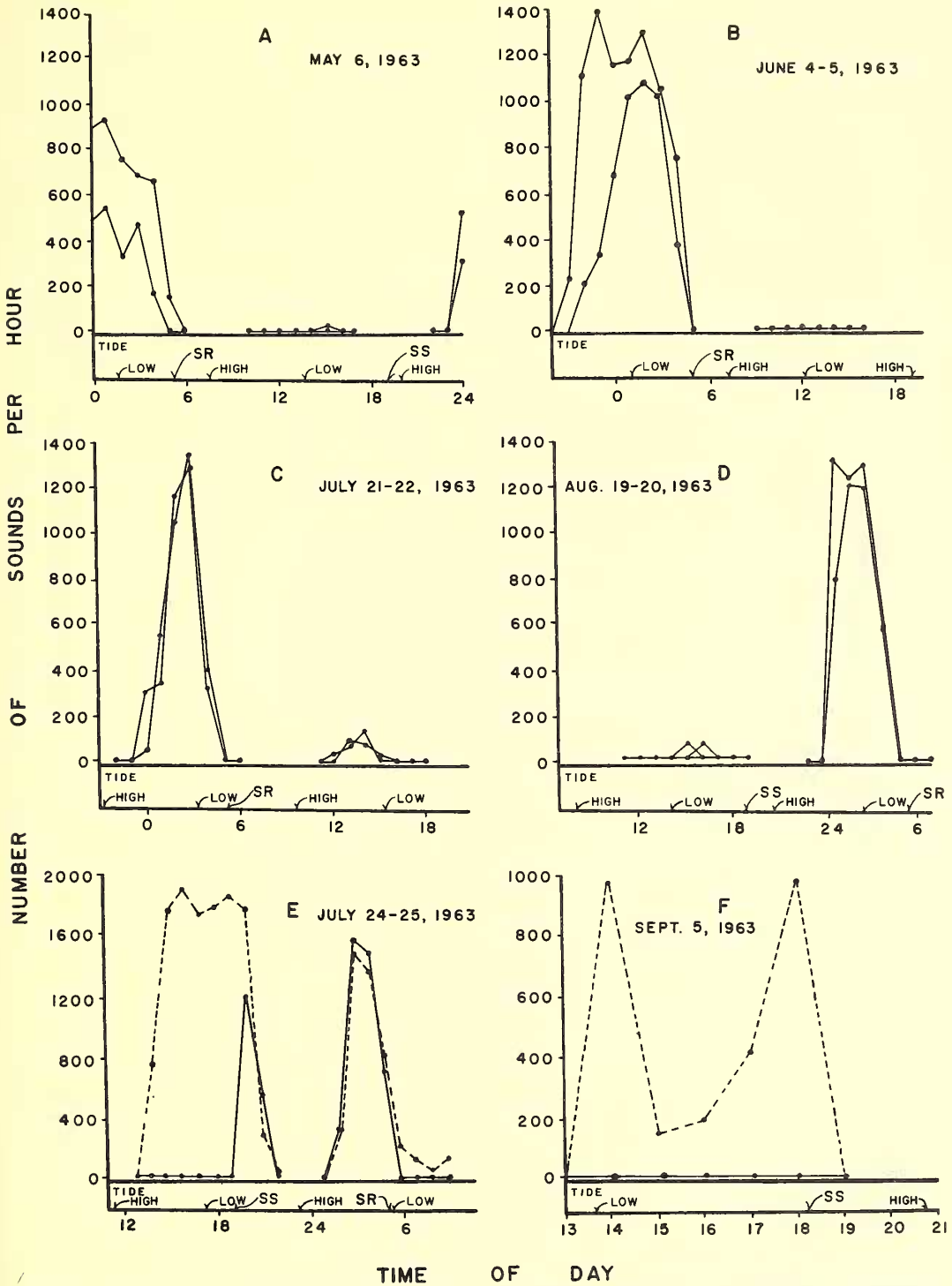
TABLE 13. NUMBER OF SOUNDS AND TIME OF FIRST SOUND PRODUCED BY MALE *Uca pugilator* AT NIGHT DURING FOUR MINUTES WITH OR WITHOUT SOUND PLAYBACK OF 56 SOUNDS PER MINUTE<sup>1</sup>

With Sound Playback			Without Sound Playback		
Male Number	Time of First Sound (In Seconds)	Number of Sounds	Male Number	Time of First Sound (In Seconds)	Number of Sounds
1	6	84	1	None Heard	0
2	51	25	2	226	1
3	7	1	3	None Heard	0
4	80	28	4	None Heard	0
5	5	120	5	None Heard	0
6	None Heard	0	6	18	19
7	80	2	7	None Heard	0
8	6	81	8	104	16
9	20	7	9	None Heard	0
10	11	51	10	23	106
11	2	106	11	None Heard	0
12	11	85	12	None Heard	0
13	164	5	13	114	12
14	11	121	14	79	17
15	9	128	15	None Heard	0
	Mean:	56.3*		Mean:	11.4
	S D:	49.3		S D:	27.2

<sup>1</sup>Fifteen different males, tested alternately, were used with and without sound playback.

\*Means differ significantly at the .01 level ( $t=3.0965$ ).





TEXT-FIG. 7. The number of sounds per hour produced by pairs of male *Uca pugilator* recorded simultaneously during low tides for a twenty-four hour period. A-D: number of sounds produced by males under normal day-night cycles; E-F: number of sounds produced by a male under a light-proof box (dashed lines) and a box covered with clear Saran wrap (solid lines). In the time scale, 0 and 24 correspond to midnight and 12 to noon. The time of high tide, low tide, sunrise (SR) and sunset (SS) are also indicated.

TABLE 14. THE MEAN NUMBER PER MINUTE AND STANDARD DEVIATION OF SOUNDS PRODUCED BY 10 MALE *Uca pugilator* AT NIGHT DURING AND AFTER THREE MINUTES OF SOUND PLAYBACK AT AN INTENSITY ONE-HALF THAT OF THE MALE<sup>1</sup>

Number of Sounds Per Minute in Playback	During Playback		After Playback	t-Value
	Mean:	SD:		
16	Mean: 16.9		16.0	0.69*
	SD: 4.5		2.9	
24	Mean: 16.7		17.9	0.92*
	SD: 8.3		4.7	

<sup>1</sup>Two different groups of ten males were used with each different playback.

\*No significant difference between means during and after the playback.

ended shortly before sunrise but when the tide was still quite low. The results of simultaneous recordings of pairs of males, one under a light-proof and the other under a clear-topped box, are shown in Text-fig. 7-E. On July 24-25 the male under the dark box (dashed lines) produced sounds during the day as well as at night from 1300 to 2200 hours while the male under the clear-topped box produced no sounds until after sunset. Both crabs stopped producing sounds when the tide approached their burrows (2200 hours) and started again when the tide retreated (0100 hour). The male under the clear-topped box stopped producing sounds again just before sunrise, while the male under the dark box continued to produce sounds, though at a low rate. The experiment was repeated for a six-hour period in September with another pair of males (Text-fig. 7-F). The male under the light-proof box continued to produce sounds during the day but at a lower rate, possibly reflecting the decline in reproductive activity in the colony during this time. No sounds were produced by the control crab.

No sounds were detected in recordings with a hydrophone during high tide periods during the day or at night. However, it is quite possible that the hydrophone might not have detected sounds produced in the burrows after the burrow entrances were sealed closed with sand plugs by the crabs.

The effect of light on sound-producing males at night is shown in Table 17. The 10 experimental and 10 control crabs produced sounds at comparable rates two minutes before exposure to light. After the light was turned on the experimental crabs produced many fewer sounds than they did the previous two minutes but the

control crabs continued to produce sounds at the normal rate. Light also caused many males to start waving, especially if the light source was brighter than the 100 watt bulb used in experiments. One such waving male is shown in Plate V. The photograph was taken less than ten seconds after he was exposed to a 150 watt light source.

No sound production was observed at night in colonies of *U. pugnax* and *U. minax*. Usually, *U. minax* remained inside their burrows at night but some *U. pugnax* were always feeding just outside their burrows. Both species exhibited waving behavior during the day, as did *U. pugilator*.

#### IV. DISCUSSION

##### A. SEASONAL CHANGES IN COURTSHIP BEHAVIOR

Field observations in early March, 1963, suggested that male *U. pugilator* did not exhibit any courtship behavior for at least a month after hibernation ended. Since air temperatures in March afternoons were often higher than during days when courtship was observed in the summer, presumably some physiological state of the crabs rather than air temperature was responsible for this lack of reproductive activity. Temperature was almost certainly not a factor in the sudden decline of waving activity and sound production that took place in September but, rather, the cessation of courtship activity probably reflected endocrine changes.

Changes in the courtship of other *Uca* species also appear to be independent of temperature. Von Hagen (1962) reported that in *U. tangeri* nocturnal wandering and copulation were observed during June and July, 1960, and predominantly on nights of the new moon. Also, females exhibited a monthly cycle of egg development during these periods. Crane (1958) found that

TABLE 15. MEAN NUMBER AND STANDARD DEVIATION OF SOUNDS PRODUCED BY 30 MALE *Uca pugilator* UNDER LIGHT-PROOF AND CLEAR-TOPPED BOXES ONE MINUTE BEFORE, DURING AND AFTER SOUND PLAYBACK DURING THE DAY<sup>1</sup>

Box Type <sup>2</sup>	Before Playback			During Playback			After Playback		
	Mean:	SD:		Mean:	SD:		Mean:	SD:	
Light-proof	Mean: 0.0			6.5			7.8		
	SD:			8.2			7.8		
Clear-topped	Mean: 0.0			0.1			0.1		
	SD:								

<sup>1</sup>The sound playback consisted of 56 sounds per minute.

<sup>2</sup>Thirty different males, tested alternately, were used under each box type.

TABLE 16. THE NUMBER OF MALE *Uca pugilator* IN A SCREEN PEN EXHIBITING WAVING BEHAVIOR OR SOUND PRODUCTION AT THE BURROW ENTRANCE DURING VARIOUS TIMES OF THE DAY

I. June 22, 1962: 8 Males													
	Time:	1615	1630	1700	1810	1840	1910	1945	2015	2100	2130	2200	
Waving		1	1	1	6	2	4	1	0	0	0	*	
Sound Production		0	0	0	0	0	0	2	5	3	2	*	
II. June 26, 1962: 9 Males													
	Time:	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	2100	2130
Waving		5	6	7	5	4	3	5	3	2	*	0	0
Sound Production		0	0	0	0	0	0	0	0	0	*	1	3
III. June 28, 1962: 9 Males													
	Time:	0900	0930	1000	1030	1100	1130	1200	1230	1300	1350	2330	0015
Waving		4	7	4	2	8	5	5	5	4	*	0	0
Sound Production		0	0	0	0	0	0	0	0	0	*	4	5

\*High water mark near to or over crabs which have gone into their burrows.

male *U. maracoani* showed five to six general changes in their behavior patterns over a period of days or weeks during the breeding season. The males went through periods when they remained in their burrows during low tide, then underwent wandering-nonaggressive, wandering-aggressive, territorial and, finally, a display phase when they waved and were behaviorally dominant to males in all other phases. Preliminary dissections indicated that these changes were not correlated with changes in gonadal state and Crane therefore attributed control of the phases to some other endocrine gland.

#### B. COMPARISONS BETWEEN WAVING DISPLAY IN THE THREE SPECIES

The descriptions of waving display in the three species agreed in general with those of Crane (1943.2) but there were some differences. The single jerk or several jerks she reported in *U. pugnax* as the major cheliped was returned to the front of the body were not observed. Rather, both the lateral extension and return of the chela to the front of the body appeared to be a smooth continuous gesture. I did not see the elevation of the ambulatories she reported during the wave of *U. minax* but this may have been due to the sharply sloping mud bank where field observations were carried out, which could have inhibited ambulatory movements during the wave. Our data on wave durations in the three species are comparable. However no precise quantitative studies have been published in which variation within waves of individuals or within a species have been quantified. Crane (1943.2) stated that in the study of North American species of

fiddlers, the geographic locality was of no importance. It is possible that crabs at extremes of their geographic ranges might show differences in display.

Differences in group waving display in the three species can be correlated with their evolution within the genus. Crane (1943.2), on the basis of anatomical and behavioral evidence, placed *U. pugnax* and *U. minax* in her "group 2" species which she characterized as relatively primitive, mud-dwelling forms exhibiting lethargic courtship and locomotory movements. Males in these species waved far less than *U. pugilator* and it appeared that waving depended more on the actual sight of the female in these species. *Uca pugilator*, in contrast, show anatomical affinities to the more advanced species (Crane,

TABLE 17. THE MEAN NUMBER PER MINUTE AND STANDARD DEVIATION OF SOUNDS PRODUCED BY 10 MALE *Uca pugilator* AT NIGHT BEFORE AND DURING EXPOSURE TO LIGHT

Group of Ten Crabs <sup>1</sup>		Minutes	Minutes	t-Value
		1, 2	3, 4	
Experimental Crabs	Mean:	21.5	5.4	7.55*
	S D:	8.4	4.5	
Control Crabs	Mean:	19.2	17.4	0.79
	S D	6.2	8.1	

<sup>1</sup>Experimental crabs: Two minutes of darkness followed by two minutes of light. Control crabs: Four minutes of darkness.

\*Means before and during light differ significantly at the .01 level.

1943.2) and devote much more time to waving when females are not present. It was possible to demonstrate that other stimuli such as sounds from courting males caused male *U. pugilator* to increase their waving rate (Table 4). Gordon (1958) reported that groups of male *U. annulipes* often started to wave rapidly in the absence of females. Similar behavior was observed in *U. pugilator*. It is possible that in these species the rapid waving of males is itself a stimulus that other nearby males emulate.

#### C. SOUND PRODUCTION BY MALE *U. pugilator* AND FEMALE *U. pugilator*

The stridulatory-like sounds from male *U. pugilator* were produced when conspecific crabs of either sex and female *U. pugilator* were introduced into the male's burrow. The fact that males of this species also produce rapping sounds similar to those used in courtship by *U. pugilator* would seem to indicate that such sounds (stridulatory) are not involved in courtship. In addition, stridulatory sounds are employed by many other species of decapods as aggressive signals (Guinot-Dumortier & Dumortier, 1960). It is hypothesized that stridulatory-like sounds produced by *U. pugilator* function as warning to an intruder that a burrow is occupied, as has been postulated by Crane (1941.2) for *Ocyropsis*.

Sound production by female fiddler crabs has been observed in *U. tangeri* by Von Hagen (1962) and the sounds were produced in aggressive interactions between females. It is probable that the sounds produced by female *U. pugilator* have a similar function although they may also be involved in other behavior patterns.

#### D. COURTSHIP INTERACTIONS BETWEEN MALES AND FEMALES

The introduction experiments involving females placed before the burrows of male *U. pugilator* showed that the initial presence of a female would cause males to increase their waving rate more than twofold (Table 1). A moving female was capable of eliciting even more rapid waving movements (Table 2). Non-moving females lost the ability to induce waving in males within 30 seconds and were attacked by 13 of the 30 males tested. The males abruptly ceased their attacks and began waving when females were moved during the experimental period. These experiments demonstrated that lateral movements by the female stimulated the males to wave for prolonged periods (over 30 seconds). Von Hagen (1962) previously showed that in addition to lateral movement, vertical movements of females and models stimulated waving in *U. tangeri*.

The waving responses of male *U. pugilator* to females of different species before, during and after they were moved before their burrows were similar to the responses to conspecific females under the same experimental conditions (Table 3). Burkenroad (1947) observed that *U. pugilator* waved at *Sesarma* sp. which wandered into the colony. Von Hagen (1962) found that *U. tangeri* would wave at *Carcinus maenas* and *Pachygrapsus marmoratus*. It appears that males of *U. pugilator* and *U. tangeri* cannot discriminate between females of different *Uca* species, and in fact treat any crab approximating their size but lacking the major cheliped, as females. These results support the hypothesis that selection of a conspecific mate must be accomplished by the female, at least during the initial stages of courtship. However, experiments which demonstrate a selective response by females for conspecific males are lacking for any species of *Uca*.

The courtship behavior of male *U. pugilator* during the day changed according to the distance of the female from the male's burrow (Text-fig. 6). At distances of 5 to 10 cm. between the female and the burrow, more waves than sounds were produced by the males. At 5 cm., the number of sounds increased and at 2.5 cm. many more sounds than waves were produced. Observations of courtship interactions when the females were farther than 10 cm. from the burrow showed that only waving took place. It follows then that the initial stages of courtship by the male during the day consist of waving display. Sound production occurs only after the female has come closer to the burrow. The data from Table 6-A suggested that the relative amount of waving and sound production was modified by the pace at which the female approached the male's burrow. A slowly approaching female would remain farther from the male's burrow for a longer period of time and the male would tend to produce a greater number of waves. Sound production by the male could be observed just outside the burrow entrance after the slow approach of the female. If the female approached quickly, fewer waves were produced and sound production was confined to the inside of the burrow. Burkenroad's (1947) contention that diurnal sound production occurred only when the male was inside his burrow would seem to apply only when the female approached quickly.

Introductions of males and females into the burrows of a male at night caused the rate of sound production by the test males almost to double (Table 9). Sounds were produced at comparable rates immediately after similar introduction tests during the day. These data indi-

cate that sexual discrimination inside the burrow does not take place. Under natural conditions sexual discrimination appears to depend on cues which occur earlier on the beach surface. Several workers (Burkenroad, 1947; Altevogt, 1957; Salmon & Stout, 1962) have demonstrated that during the day sexual discrimination by the male is based on visual cues, *i.e.*, the presence or absence of the major cheliped. Field observations in this study showed that sexual discrimination at night depended on the intensity of contact between male and intruding crab. Gentle tactile stimulation elicited courtship behavior consisting of higher rates of sound production, movement into the burrow and leg flicking movements by the male. More intense contact resulted in the cessation of sound production and aggressive behavior. Gentle tactile stimulation with a variety of objects and with a leaf of *Spartina* (Table 8) also elicited courtship behavior from the males, which indicates that chemical cues are secondarily involved (if at all) in the initial stages of nocturnal courtship and in sexual discrimination.

Burkenroad (1947) stated that sounds produced by the male after a female approached his burrow during the day differed from sounds produced by lone males at night only in that the intersound intervals were smaller. But he did not physically analyze the sounds for other differences. When sounds produced by males at night, before and during introduction experiments, were analyzed, the pulse composition was more variable (Table 10) and the interpulse intervals were shorter during the introduction (Table 11 and Plate III). It is likely that these changes would also characterize sounds produced by males when approached by females during the day, since in both cases the sounds emanate from males that are sexually stimulated. It would be of interest to determine if *U. pugilator* is capable of discriminating between sounds of various pulse composition. Since *U. tangeri* normally produces two types of sounds (long and short whirls) which differ in their pulse number, it is quite likely that these differences can be detected and may have communicative value in both *U. tangeri* and *U. pugilator*.

#### E. EFFECT OF LIGHT AND TEMPERATURE ON COURTSHIP BEHAVIOR

The behavior of males isolated in screen pens (Table 16) and the results of diel recordings (Text-fig. 7) confirmed Burkenroad's (1947) original hypothesis that waving was confined to diurnal and sound production to nocturnal periods. The tallies of per minute sound production by individual males at night (Table 7) indicated

that the sounds were produced almost continuously, although there were occasional periods from a few seconds to five minutes when sound production stopped temporarily. The experiments in which males were covered with light-proof boxes (Text-fig. 7) and exposed to artificial light at night (Table 17) showed that these changes in courtship behavior were controlled and synchronized principally by changes in the daily light cycle. The response of males to sound playbacks of 56 sounds per minute was also controlled by light. During the day, the response of males consisted of an increase in waving rate (Table 4) but when covered with a light-proof box, of sound production (Table 15).

An influence of temperature on rate of waving has been reported by Von Hagen (1962) for *U. tangeri*. There was a gradual and linear increase in the average rate of "spontaneous" waving (waving in the absence of females) from 2 to 14 waves per 30 seconds at body temperatures of 17° to 44° C. These results indicate that an adequate description of waving rate in any *Uca* species must include data on temperature conditions. Similar measurements were not made in *U. pugilator*, as it was not possible to control for the influence of females or for sound production from neighboring males on the waving rates of individual males. Attempts to control for possible visual stimuli by surrounding a male's burrow with an opaque screen resulted in complete inhibition of waving. Von Hagen (1962) found that at any one temperature the number of waves and short whirl sounds produced by the males for a 10-second period were similar. His measurements ranged from 1.9 sounds and 2.0 waves per 10 seconds at 21° C. to 4.4 sounds and 4.5 waves at 38° C. The average rate of sound production by lone male *U. pugilator* at 20° C. was 18.5 sounds per minute or about 3 sounds per 10 seconds. It is possible that the slower rate of sound production by *U. tangeri* at temperatures comparable with *U. pugilator* is an adaptation to the higher daily temperatures in Andalusia than at Beaufort. The data in Text-fig. 4 show that there was a correlation between higher temperatures and an increase in the mean rate of sound production by males at night. Since an increase and decrease in temperature from one day to the next was correlated with similar changes in rate of sound production, it is likely that temperature casually affected rates of sound production. Field observations revealed that at colder temperatures the cheliped of a sound-producing male was raised and lowered much more slowly. It would be expected therefore that the time between successive contacts between the claw and the substrate (the interpulse interval) and the total

amount of time involved in the production of a single sound (the sound duration) would increase. The results of physical analysis of sounds produced at lower temperatures showed that these were the principal changes that occurred (Text-fig. 5 and Plate II).

#### F. CHORUSING BEHAVIOR

Alexander (1960) defined chorusing in orthopterans and cicadids as the tendency for ". . . neighboring males in colonies to synchronize, alternate or combine in some unusual fashion, the individual phrases or pulses of their songs." He stated that the simplest kind of chorusing behavior consisted merely in the starting of song by large numbers of individuals in a colony in response to hearing other individuals start.

There is evidence for chorusing behavior between males of *U. pugilator* under natural and under experimental conditions. The rate of sound production by groups of males at night was observed to increase when a nearby male, probably in response to tactile stimulation by another crab, increased his rate of sound production. In addition, previously silent males in the vicinity began to produce sounds. Sound playbacks of 56 sounds per minute induced sound production more quickly in males previously frightened into silence (Table 13). Males producing sounds before the playback responded preferentially to sound playbacks at this rate by increasing their own rate of sound production during the playback (Table 12). Males also showed a significant increase in rate of sound production during the playback of 24 sounds per minute. The range in increase of sound production rate between control and experimental periods during this playback was 4.7 sounds per minute, only 1.6 sounds per minute over the range of increase during the control test when no playback was made. It is possible that the increase during the playback of 24 sounds per minute was a chance phenomenon. Further experiments are needed to clarify that problem.

Although it was possible to demonstrate induction of sound production in silent males as well as an increase in rate of sound production during certain playbacks, there is no evidence for more complex chorusing behavior involving synchrony or alternation of sounds between males. Three-minute playbacks at rates of 16 and 24 sounds per minute, comparable in rate to many males in the field, did not influence the mean rate of sound production by the males tested (Table 14). In addition, synchrony or alternation of sounds between neighboring males was never observed in the field.

When sounds at a rate of 56 per minute were

played back to males during the day, courtship behavior was also influenced. Males previously frightened into their burrows responded to the playback by coming to the surface faster than males which received no playback (Table 5). Both Dembowski (1925) and Von Hagen (1962) have reported that *U. pugilator* and *U. tangeri* in their burrows responded similarly to sound production by other crabs in the field. Those males already on the surface (as well as those induced to come out of their burrows) responded to playbacks by increasing their rate of waving (Table 4). The results parallel those of sound playbacks at night, as in both cases there is an increase in the rate at which courtship movements are produced as well as in the number of males exhibiting courtship behavior.

There is some indication that visual stimuli in addition to sounds are involved in chorusing behavior. Gordon's (1958) report of synchronous claw waving in *U. annulipes* between groups of males in an area within the colony (also observed in *U. pugilator*) indicates that the males can be stimulated to wave faster even when no females are present. Presumably the stimulus involved here is one or more males waving faster than others. But experimental evidence to support this hypothesis is lacking.

#### G. THEORETICAL ASPECTS

Courtship in *U. pugilator* appears to be composed of at least two phases. The "calling" phase consisted of waving behavior during the day, and sound production at night, both exhibited by males in the absence of females. The "courting" phase, in contrast, was released and maintained in males only by the presence of the female. During the day the courting phase consisted of rapid waving when the female approached and rapid sound production starting just before and after she entered the male's burrow. At night the courting phase consisted of rapid sound production accompanied by leg flicking movements, released in the male by tactile stimuli from the female.

There is strong evidence that in *U. pugilator* waving is primarily involved in courtship. Intruding females cause an increase in waving rate while intruding males cause previously waving males to cease waving and defend their burrows. It is probable that waving serves at least three functions: orienting the female to the male's burrow, stimulating her sexually and presenting cues which identify conspecific males.

The sounds produced by males at night during the calling phase are almost certainly directed at the female. Both sexes initiate sound production at rapid rates when they touch a resi-

dent male. Sexual discrimination at night appears to depend upon behavioral cues which occur after this initial contact. The hypothesis that sounds are attractive to the female is supported by experiments of Von Hagen (1962). In two cases he was able to induce female *U. tangeri* which had paused near a male's burrow, to enter the burrow when artificial sounds simulating those of males were played back. The negative results in sound playback experiments to female *U. pugilator* in this study may be due to a number of factors, *i.e.*, there was no way to determine before the experiment if the females had copulated previously. In addition, they were tested almost immediately after being subjected to the trauma of handling and were only given one minute to respond to the playback. Better-designed experiments with females need to be conducted, preferably in the field and with females raised in the laboratory or isolated from males immediately after hibernation. Females may respond to sounds produced by males at night in several ways. It may be possible for females to orient directionally to the sound-producing male by comparing the intensity of vibrations perceived on the side of the body nearest the male with vibration intensities on the other side. The sounds might also induce more rapid wandering activity by receptive females which, in dense colonies of males, would increase the probability of contact with the male.

There is considerable variability in both the rate at which sounds are produced by *U. pugilator* at any given temperature (Text-fig. 4) and in the intervals between successive sounds in a series. Alexander (1960, 1962) has pointed out that the evolution of precise temporal song patterns in male orthopterans is selected for when more than one sound-producing species lives in a particular area. The variability in calling sounds of *U. pugilator* can therefore be attributed to its isolation from other species which utilize sounds in a calling phase. There is some evidence from introduction experiments that rapping sounds are produced by courting male *U. pugnax* but only when the males are deep inside their burrows. Under these conditions acoustical interference with neighboring male crabs would be minimal. Although there is considerable overlap in their ranges, the two species are found in different habitats. Usually, *U. pugnax* is found in muddy areas and *U. pugilator* on sandy beaches. Teal (1958) has demonstrated that larvae of *U. pugnax* and *U. pugilator* tend to select the substrate in which the adults are found. Miller (1961) found that the mouth parts of adult *U. pugnax* and *U. pugilator* show species-specific modifications of the spoon-tipped

hairs used in feeding which enables the adults to feed most efficiently on the substrate preferred by the larva.

The evolution of specific song patterns of male orthopterans develops simultaneously with a corresponding specificity in response to the male by the female (Alexander, 1960). Walker (1957) has shown that in certain tree crickets (Oecanthinae), the females respond preferentially to the pulse rate of conspecific males. Since the pulse rate changes with temperature, a positive response by the female occurs only if her body temperature is approximately that of the male. In these insects the pulse rates increase regularly at higher temperatures and with little deviation from the mean. The rate of sound production and the intervals between sounds produced by *U. pugilator* are variable at temperatures encountered in the field. It is likely that the female shows little specificity for these properties in the calling sounds of the male. In addition, the type of chorusing behavior found in *U. pugilator* in which neighboring males can stimulate each other to produce sounds at night is characteristic of orthopteran species in which there is no precise rhythm in the calling song (Alexander, 1960).

At least eight species of *Uca* are known to produce sounds during their day-time courtship. None of the six tropical American rapping species exhibit courtship behavior or produce courtship sounds at night (Crane, personal communication). On the basis of present evidence it appears that only in *U. pugilator* and *U. tangeri*, which extend their ranges into temperate areas, does nocturnal courtship occur. It seems logical to postulate that in temperate regions, climatic conditions limit the periods when successful reproduction can take place and that any mechanism which increases the rate of fertilization would be of great selective value to a temperate species. The incorporation of acoustical signals into nocturnal courtship of these two species enables reproductive activities to occur at night, independent of visual cues such as waving, which are effective only during the day. The results of field observations during the breeding season indicate that climate does not directly affect the reproductive activities of adult *U. pugilator* and *U. tangeri*. Giese (1959) stated that the life cycles of marine invertebrates were usually timed so that the environment favored optimal survival of the young. Booloottian *et al.* (1959), in their studies of the reproductive cycles of five west coast species of crabs, found that in three of the species studied reproductive activities of the adults were correlated with the availability of food during the larval stages. It would be in-

teresting to learn if the reproductive activities of temperate *Uca* also showed this correlation.

Male *U. tangeri* undergo a wandering phase and migrate to the entrance of the female's burrow where sound production and copulation may follow. Von Hagen (1961, 1962) has suggested a possible explanation for this courtship pattern. Customary claw harvests by local inhabitants strip many males of their major chelipeds. As a result many males possess a small claw and a regenerating major cheliped, much reduced in size. It may be that males lacking the major cheliped cannot produce sounds of sufficient intensity to communicate to females from a distance. Migration to the female's burrow could be an adaptation to bring the sexes closer together before sound production occurs. In addition, males of this species are able to produce sounds without the large major cheliped. These unusual reproductive patterns for a broad front fiddler crab may be, as Von Hagen (1961, 1962) has suggested, a cultural product of man.

In contrast, courting males of *U. pugilator* confine their activities to the burrow and the area surrounding the entrance, which they defend against intruders. It is likely that, as is the case in territorial sound-producing male orthopterans, the male's waving during the day and his sounds at night function to attract the female into the male's territory where copulation takes place. Burkenroad (1947) observed a total of eleven mating couples at night near the water's edge during low tide, a considerable distance from the sound-producing males found in the upper portion of the beach. But Crane (personal communication) believes that in such cases insertion of the male abdominal appendages into the female's genital aperture probably does not take place.

Crane (1957) pointed out that in the more advanced species of broad fronts much more time was devoted to waving display. But she did not present any evidence to support her conclusion or suggest any causal mechanisms responsible for this change in behavior. The results of experiments reported here have shown that courtship in male *U. pugilator* is augmented by sound stimuli emanating from other males both at night and during the day. Synchronous claw waving by groups of males during the day, in the absence of sounds, indicate that visual stimuli may also augment courtship activity. It is postulated that sounds and visual stimuli from male *U. pugilator* are responsible for the greater time devoted to courtship activity by neighboring males. In *U. pugnax* and *U. minax*, these cues do not appear to operate and courtship by males appears to depend more strongly on the

actual sight of the female. Alexander (1960) has found in the orthopterans and cicadids that although the basic function of the male's sounds is to attract a receptive female, the "... sounds actually have a greater variety of effects upon other males which hear them than upon females." He attributed these "side" effects to selection for chorusing behavior patterns which enhance the primary function of bringing the sexes together through adjustments in the social organization of the species.

The disagreement in the literature concerning the function of waving is due in part to the fact that the majority of the studies have been purely descriptive. While a great deal of valuable information has been contributed by such studies, few authors have employed experimental techniques or quantified their observations. As a result most of what is known about courtship in *Uca* is based upon subjective interpretation of field observations. In addition, most of the studies have dealt only with waving, the initial stage in courtship, to the exclusion of subsequent courtship interactions inside the burrow which might also yield important clues to relationships between species. More extensive experimental studies on the behavior of each species are needed before generalizations can be applied with a degree of certainty. Indeed, generalizing at this point may risk masking a variety of behavioral adaptations evolved within each species during their courtship.

## V. SUMMARY

1. The role of waving behavior and sound production in the courtship behavior of *Uca pugilator* was studied at Beaufort, North Carolina, during the summers of 1962 and 1963. Comparisons were made between the waving displays of *U. pugilator* and two local species, *U. minax* and *U. pugnax*, and between the acoustical behavior of *U. pugilator* and the European species, *U. tangeri*.

2. When no female was present, waving behavior by male *U. pugilator* was confined to males with burrows during diurnal low tides. At night, sound production occurred during low tides and almost continuously by lone males possessing burrows. When light-proof boxes were placed over the males, sounds were produced during the day. Conversely, exposure to artificial light at night caused sound production by males to stop within 30 seconds.

3. Waving rates of male *U. pugilator* more than doubled when they were presented with conspecific females or females of different *Uca* species. When a female approached within 7.5 cm. of a male's burrow the male began to pro-



duce sounds between consecutive waves. If the female followed the male into his burrow the male produced many sounds at a rapid rate.

When a sound-producing male was touched by a female at night, his rate of sound production nearly doubled and equaled the rate of which sounds were produced during the day. Gentle tactile stimulation with a variety of inanimate objects elicited the same response from the test male. When touched by an intruding male at night, the resident male at first increased his rate of sound production, but subsequently stopped sound production and defended his burrow against the intruder.

4. Sound playback experiments to determine if females were attracted to sounds produced negative results. Playbacks to males demonstrated that they would at night increase their rate of sound production when the playback consisted of 56 sounds per minute, the fastest rate recorded in the field. Playbacks at slower rates did not affect the rate of sound production by the test males. Playbacks of 56 sounds per minute also induced males previously frightened into silence to produce sounds faster than control males not exposed to playback. During the day playbacks induced males in their burrows to come to the surface and those males already on the surface to wave at faster rates. The significance of these responses by the males to playbacks was discussed and the results compared to certain types of chorusing behavior shown by male orthopterans and cicadids.

5. Sounds produced by male *U. pugilator* before and after contact with a female were physically analyzed. It was found that the sounds after contact with the female were produced at greater rates, had smaller interpulse intervals, had a more variable pulse content per sound but contained about the same mean number of pulses per sound.

6. The rate of sound production in the field by lone male *U. pugilator* at night was found to increase gradually with higher temperatures. But there was a considerable variation in both the rate at which individual males produced sounds and in the intersound intervals at any one temperature. The theoretical significance of this variability was discussed with reference to the specificity of the female to sounds of the male and was attributed to the ecological isolation of *U. pugilator* from other sound-producing species.

7. The waving display of *U. pugilator* differed from *U. pugnax* and *U. minax* in the duration of single waving movements, in the movements of the ambulatories and the minor chelae and in

body movements which accompanied each wave. In addition, waving by *U. pugilator* occurred much more frequently than in the other two species and even when no female was present.

8. Introduction of other *Uca* into the burrows of male *U. pugnax* during the day resulted in the production of stridulatory-like sounds. In two cases, rapping sounds similar but not identical to those of *U. pugilator* were heard. It was hypothesized that the stridulatory-like sounds were involved in aggressive behavior while the rapping sounds were involved in courtship behavior. No sounds were detected at night from male *U. pugnax* or *U. minax*.

Burrow-owning female *U. pugilator* produced sounds in response to intruding females by alternately striking the ground with their two minor chelipeds. It was hypothesized that these sounds were also used as aggressive signals.

9. It was hypothesized that the presence of nocturnal courtship and sound production, in addition to diurnal courtship exhibited by most *Uca*, was an adaptation of temperate species which enabled faster completion of reproductive activities during the brief periods when climatic conditions were favorable for the survival of the young. The ecological factors which account for the differences between nocturnal and acoustical behavior of *U. pugilator* and *U. tangeri* were discussed.

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## EXPLANATION OF THE PLATES

## PLATE I

- FIG. 1. Photograph of a male in position and producing sounds at night just outside the entrance to his burrow.
- FIG. 2. The burrow entrance (left) and adjacent impression (right) left in the sand by the base of the major chela of another male which had been producing sounds for three previous hours.

## PLATE II

- FIG. 3. Sonogram of one sound produced by a male *Uca pugilator* at 14° C. (A), 18.5° C. (B) and 24° C. (C).

## PLATE III

- FIG. 4. Sonogram of two sounds produced at night by a male *Uca pugilator* before (A) and during (B) introduction of a conspecific female into his burrow, illustrating the re-

duction in the interpulse intervals of sounds produced during the introduction. Pointed lines in A are the same length as those in B, but in B they extend farther into adjacent pulses.

## PLATE IV

- FIG. 5. Sonogram of a sound produced by a male *Uca pugnax* during the introduction of a conspecific male (A) and by a female *U. pugilator* during the introduction of a conspecific female (B). Both introductions were made into the burrow of the test crabs during the day.

## PLATE V

- FIG. 6. A male *Uca pugilator* waving at night. The male had previously been producing sounds but started to wave ten seconds after exposure to a 150 watt incandescent light source.